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ON THE DISTRIBUTION OF RED COLOR IN VEGETATIVE PARTS IN THE NEW ENGLAND FLORA.

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THE meaning of red color in the vegetative parts of plants is a subject which very early attracted attention. Beginning with Grew (1677), many observations and experiments have been made, resulting in several theories. Von Mohl¹ (1837) was the first of modern botanists to study the subject with thoroughness, concluding, according to Overton's review of his work, that red color is an incidental result of cooler temperature and intense light. Kuntze² (1877), on the other hand, gave an ecological significance to red color, considering it a protection against animals. Stahl³ (1888) showed that animals usually choose green leaves first, but if hungry eat either green or red leaves. Since this happens in the dark as well as in the light, some difference in the nourishing qualities or in the taste of the red leaves seems to be the determining factor of the choice. Pick⁴ (1883), according to Stahl, held the theory that red color favors the breaking up and change of starch into sugar, by absorbing the light rays injurious to this change. Kerner⁵ thought the intense light is harmful to the plant, being destructive to young chlorophyll, and that the red color forms a screen, thus permitting the change and passage of food materials. Engelmann⁶ (1886) gave no positive meaning to erythrophyll, for it seemed sufficient to him that assimilation takes

¹ Untersuchungen über die winterliche Färbung der Blätter. Included in *Vermischte Schriften* 375-392.

² Schutzmittel der Pflanzen gegen Tiere und Wetterungunst. *Gratisbeilage zur Bot. Zeit.* Leipzig, 1877.

³ Pflanzen und Schnecken. *Jenaisch Zeitsch. Nat. u. Med.* 22.

⁴ Bedeutung des rothen Farbstoffs bei den Phanerogamen und die Beziehung desselben zur Stärkewanderung. *Bot. Centralbl.* 16:281.

⁵ *Natural History of Plants* (transl. by Oliver) 1: 101-103, 364-366, 483-499.

⁶ Die Farben bunten Laubblätter und ihre Bedeutung für die Zerlegung der Kohlensäure im Lichte. *Bot. Zeit.* 45:449.

place, but little retarded by the loss of light. Stahl⁷ (1896) agreed with Kerner and Pick in the belief that the red color is a device for promoting the change and passing of food stuffs, not however in its use as a light screen, but by raising the temperature of plant tissues through its property of converting light into heat; cold delays these processes. This warming up of the plant also favors transpiration, an ecological factor as important in Stahl's view as the one mentioned. Overton⁸ (1899) presented the theory that the red color is a glucoside compound, produced as a result of sugar concentration in the cell, under the influence of intense light and cool temperature. He assigned no distinct ecological significance to red color and in reality gave us a theory which is a modification of Von Mohl's. MacDougal⁹ (1896) has given a good popular account of the theories concerning red color.

Little attention has been given to the study of red color in the eastern United States. Stahl and Overton cite this region with the Alps as offering the best conditions by far for a great display of color. No attempt, so far as I can find, has been made anywhere to study comprehensively the red color in summer foliage, or, in fact, to work up the subject at all in a statistical way, and therefore with a view to seeing how far statistical observations made in New England may agree with the principal theories this study is offered. Thanks are due to Mr. M. L. Fernald, of the Gray Herbarium, for naming many plants, and to Dr. W. F. Ganong, of Smith College, with whose kind assistance and direction the working out of the data was done.

The plants examined were gathered at random in Northampton and vicinity, Springfield, Warren and Woods Hole, Mass., and in Squirrel island, Maine. The proportion of situations, dry and wet, shady and sunny, from which the specimens were taken was about the same. At first only those plants were

⁷ Ueber bunte Laubblätter. *Ann. Jard. bot. Buit.* 13 : 137.

⁸ Beobachtungen und Versuche über das Eintreten von rothen Zellsaft bei Pflanzen. *Prings. Jahrb.* 33 : 171.

⁹ Physiology of color in plants. *Pop. Sci. Monthly* 49 : 1.

noted which showed red color. After most of the data were taken it was realized that the number of specimens lacking red color, but growing in the same situations, was needed for comparison, especially for determining what per cent. of our flora showed red color and what situations produced the greatest proportion of cases. Last summer a record was kept of the number of plants found on Squirrel island, Maine, an island two or three miles in circumference. The total number was 126, of which 102 showed red color; 24 showed *none at that time*, 5 of them being evergreens. Most of these 24 plants were recorded red at other times in other places. These figures, though true for a very limited region, give evidence that red color is more widely prevalent than would be supposed.

The data taken gave the name of the place, situation in which the plant was gathered, whether roadside or woods, whether wet or dry, the amount of shade, height of the plant, part colored, the date, and, as far as was ascertainable by microscopic examination, in what tissues the red color was located. The fact should be emphasized that the date at which the plant was gathered made a decided difference in the color. Owing to the length of the records taken only the results are given here.

In analyzing the results, attempt has been made to think of every possible interpretation of the presence of the color, and to ascertain by percentage how many specimens confirm each.

The first records consider *the part* of the plant in which the red occurs. Of 285 plants showing red, the stem has 211 cases (73.3 per cent.), the petiole 140 (49.1 per cent.), the leaf (mesophyll) 99 (35 per cent. of which 7 per cent. were young leaves), and the veins 66 (23 per cent.). Red color, therefore, is more common in stems than in leaves.

In upright stems more red, or red only, was shown evenly distributed in 138 cases (65.4 per cent.), near the ground in 31 (14.7 per cent.), at the nodes in 23 (10.9 per cent.), at the tip in 3 (1.4 per cent.). Red color, therefore, is not commonly localized, but evenly distributed. Cases where more red was

shown on one side of an upright stem than on another were found to be where light was brighter on the red side.

In creeping stems and inclined branches there was more red on the upper surface in 12 cases (5.7 per cent.), and on the lower surface in one case (1 per cent.).

Of 140 *petioles* more red was shown on the upper surface in 53 cases (38 per cent.), evenly distributed in 46 (32.8 per cent.), near the base in 39 (28 per cent.), on the lower surface in 10 (7.1 per cent.), near the blade in 5 (3.5 per cent.). In petioles, therefore, red color is most frequent on the upper surface, but nearly as often evenly distributed, while some petioles show a tendency to color toward the base.

Of 65 *veins* more red was shown evenly distributed in 32 cases (49.2 per cent.), on the upper surface in 18 (27.7 per cent.), on the lower surface in 15 (23.1 per cent.). It follows, therefore, that in veins, as in stems, the red color is evenly distributed in the majority of cases, and that there is more color on the upper than on the lower surface.

Of 99 *leaves* (mesophyll) more color was shown evenly distributed in 33 cases (33.3 per cent.), on edge in 20 (20.2 per cent.), on upper surface in 18 (18.1 per cent.), at tip (mostly young) in 15 (15.1 per cent.), on lower surface in 14 (14.1 per cent.), at base near petiole in 11 (11.1 per cent.). The conclusions, therefore, are that cases of even distribution are in the majority; that there is more color on the upper than on the lower surface, and on the edge than near the tip.

In a large number of cases the red color was seen on flower stems, bracts, and scales, but because these could not be ascertained for all plants the results were not tabulated. Buds, stipules, spines, tendrils, and a few roots were also found colored red. Out of the 285 specimens 26 were streaked or mottled in some way.

The next records consider the color distribution in relation to external conditions, as light, etc. Of the 285 plants examined 150 (52.6 per cent.) were gathered in dry sunny places, 61 (21.4 per cent.) in dry shady places, 40 (14 per cent.) in wet

sunny places, 34 (12 per cent.) in wet shady places. Dry situations, therefore, result in more color than wet ones; sunny situations in more than those that are shady; dry and sunny have far the most of all; and wet shady the least of all.

Of 211 *stems* 120 (56.8 per cent.) showed red in dry sunny places, 44 (20.8 per cent.) in dry shady places, 31 (14.7 per cent.) in wet sunny places; 16 (7.6 per cent.) in wet shady places.

Of 140 *petioles* 70 (50 per cent.) showed red in dry sunny places, 31 (22.1 per cent.) in dry shady places, 22 (15.8 per cent.) in wet shady places, 17 (12.1 per cent.) in wet sunny places.

Of 65 *veins* 31 (47.7 per cent.) showed red in dry sunny places, 14 (21.5 per cent.) in dry shady places, 12 (18.5 per cent.) in wet sunny places, 8 (12.3 per cent.) in wet shady places.

Of 99 *leaves* (mesophyll) 48 (48.4 per cent.) showed red in dry sunny places, 19 (19.1 per cent.) in dry shady places, 18 (18.1 per cent.) in wet shady places, 14 (14.1 per cent.) in wet sunny places.

The proportion of red in the parts of the plant is about the same for the plant itself; greater number of cases in dry places than in wet; in dry sunny places the largest percentage of all. Dry shady and wet shady places showed about the same number of cases.

An interesting confirmation of these percentages is found in reckoning them theoretically. For example, if 21.4 per cent. of the 285 plants were found growing in dry shady places, out of the 211 specimens showing red on the stem 45 should show it in dry shady places; and 40 did show it.

In dry shady places the numbers expected and attained were as follows: stems 45-44; petioles 30-31; veins 13-14; leaves (mesophyll) 21-19.

In dry sunny places the numbers expected and attained were as follows: stems 111-120; petioles 73-70; veins 33-31; leaves (mesophyll) 52-48.

In wet shady places the numbers expected and attained were as follows: stems 21-16; petioles 17-22; veins 7-8; leaves (mesophyll) 13-18.

In wet sunny places the numbers expected and attained were as follows: stems 33-31; petioles 19-17; veins 8-12; leaves (mesophyll) 13-14.

In sunny places the number of red stems is considerably larger than expected, and in wet shady places the number of red leaves is larger; otherwise the numbers expected and attained are about the same. Percentages might also be worked out for the number of specimens showing red on the stems, near the ground, at joints, etc.

In addition to the 285 plants, records were taken for 234 duplicates growing in the following situations: 129 in dry sunny places, 44 in dry shady places, 35 in wet shady places, 26 in wet sunny places. This accords with the main series except in the exchange of wet shady and wet sunny places.

To determine if the red color present in the spring and summer is a persistence of the early spring coloration, or a new feature, 109 plants were marked in the spring in different localities with copper tags. Plants were marked only when others of the same species near by were red. These were examined in summer and again in the fall, and changes recorded. One hundred plants were recorded the three times, although in some cases the marked specimen was lost and data were taken from neighboring plants of the same kind. In 54 cases red color was lost in some part; in 34 there was no appreciable change; in 28 red color was gained in some part; in 21 it was lost entirely. There was no attempt to tell how many plants without color in spring gained it during the summer or fall.

Of the 54 plants in which the red color was lost there were 36 cases (66.6 per cent.) in the leaf (mesophyll), 13 (24 per cent.) in the petiole, 12 (22.2 per cent.) in the veins, and 11 (20.3 per cent.) in the stem. Color was gained in 14 cases (50 per cent.) in the petiole, in 9 (32.2 per cent.) in the stem, in 5 (22.2 per cent.) in the veins; in 2 (7.1 per cent.) in the leaf (mesophyll).

Therefore, red color cannot be simply a persistence of spring coloration, nor is it simply an addition in the fall, for of 28 cases

of additional color 18 occurred in the summer and 10 in the fall. Color is more often lost in the leaf than in the stem, the cases of its persistence in the leaf through summer and fall being 8, of its loss 36. The percentage of increase in color is greater in stem and petiole than the loss; it is less in the leaf blade; and about the same in the veins. In order to determine in what tissues the red color is present, examination of 207 plants was made with the microscope. The following tables give the results :

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	78	35	41	12
Cortex { Hypodermis.....	38	29	15	5
Collenchyma.....	28	18	3	4
Parenchyma.....	65	49	37	16
Sclerenchyma.....	5	1	0	0
Stele { Vasc. bundles.....	3	1		
Pith.....	12			

DRY, SHADY PLACES.

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	9	6	4	0
Cortex { Hypodermis.....	8	8	2	1
Collenchyma.....	3	2	0	0
Parenchyma.....	13	9	9	2
Sclerenchyma.....	2	0	0	0
Stele { Vasc. bundles.....	1	0		
Pith.....	5	1		

DRY, SUNNY PLACES.

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	48	18	20	6
Cortex { Hypodermis.....	18	9	8	3
Collenchyma.....	15	9	2	1
Parenchyma.....	29	19	16	4
Sclerenchyma.....	0	0	0	0
Stele { Vasc. bundles.....	1			
Pith.....	3			

WET, SUNNY PLACES.

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	15	7	10	6
Hypodermis.....	10	8	3	1
Collenchyma.....	8	5	1	3
Parenchyma.....	13	9	5	8
Sclerenchyma.....	2	1	0	0
Vasc. Bundles.....	0			
Pith.....	2			

WET, SHADY PLACES.

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	6	4	7	0
Hypodermis.....	2	4	2	0
Collenchyma.....	2	2	0	0
Parenchyma.....	10	12	7	0
Sclerenchyma.....	1	0	0	2
Vasc. bundles.....	1	1		
Pith.....	2			

DISAPPEARANCE OF COLOR IN 54 PLANTS.

	Stem.	Petiole.	Leaf-blade.	Veins.
Epidermis.....	3	7	22	6
Hypodermis.....	7	5	3	2
Collenchyma.....		8	18	8
Parenchyma.....	5			
Sclerenchyma.....				
Vasc. bundles.....				
Pith.....	2	0	0	0

In frequency of color epidermis exceeds hypodermis or parenchyma in stem and leaf-blade, but in each case the cortex shows the largest number of cases. In dry sunny places the epidermis has most color, the color gradually disappearing in the stem from the outside in. In dry shady and wet shady places the parenchyma exceeds, in wet sunny places the hypodermis or epidermis. It seems then as if sunlight tends to increase the red color in the epidermis or hypodermis. In cases of disappearance of color, the loss is greatest in the epidermis

of the leaf-blade, and in the cortex of stem and petiole. In 26 cases of loss, the conditions had changed since spring from sunny to shady. This would make it seem as if red might be a protection from intense sunlight, but in 28 cases of appearance of color 13 were found in conditions which had changed from sunny to shady, and 5 were found in conditions which had changed from wet to dry. One might conclude that change of conditions favors change in color, from green to red or red to green, as has been asserted by others.

Most of the plants with red color were gathered in dry sunny places. This does not accord with observations of Stahl, who finds in moist or shady places the most noticeable red coloring. His theory does not seem applicable to the facts just given, for the conditions of sunlight and warmth in this case favor photosynthesis and conduction, also transpiration. The percentage is so large it could not be due to collecting more specimens in the spring or fall, when the temperature is lower, and thus be due to increased sugar concentration according to Overton's theory.

Taking the whole number of cases, the red color gives the largest percentages for stems and petioles, really the conducting parts of the shoot. One might think with Stahl that some advantage is derived from red color in photosynthesis and passage of food material, but again why this is needed in most of these cases is not so clear, since conditions were already sufficiently favorable for transpiration, etc. The large amount of color in the cortex seems to favor Stahl's theory also. If we apply Pick's theory, that the red color protects the conducting parts from the injurious effects of light upon the changing substances in them, we seem to have a strong argument in its favor, for the majority of the cases noted were recorded in dry, sunny places.

In wet shady places only is the percentage of cases of red color in the leaves greater than in the stems and veins. In Stahl's paper most attention is paid to color in leaves, so here is an agreement, if only a slight one, with his theory of the need of warmth to increase transpiration.

In stems, petioles, veins, and leaf-blades the largest percentages are for an even distribution of red color upon the surfaces of these parts. This would seem to show either that the shoot was evenly lighted or that some factor other than sunlight was the determining one in causing red color. However, the upper surfaces of the leaves, veins, and petioles show more color than under surfaces, and this accords with observations of others. Kerner's theory of protection from too great light, and Stahl's of increasing transpiration through the aid of red, apply here, although it is hard to see, as said before, why there is need of greater photosynthesis than is brought about by naturally favorable conditions. Overton's view is not applicable, for cool temperature is certainly not a factor in the conditions. The disappearance of red color in leaves when greater shade is present, and the great number of cases where red is located in the epidermis, are favorable to Kerner's theory of protection.

Another fact agreeing with the latter theory is in the case of upright stems, where one side, the side always toward the sun, shows often the more color. This was noticed continually in *Ambrosia*.

The red color is intensified at the joints of stems and petioles. This deepening of color, as well as that upon the upper surface of parts, is greatest in proportion in plants growing in wet shady situations. The theory of Stahl applies here, for the passing of food materials may be checked somewhat at the joint, where tubes pass into the stem; but Overton's theory applies just as well, since conduction is delayed here and sugar must be concentrated in the cells of this region. Cool temperature does not appear here however. Any theory of protection from light is not applicable, since the joints are as much shielded as the other parts of the shoot.

A large number of cases were found where the stem was very red near the ground. None of the theories seem to fit this fact.

Cases where color is absent just at the joints and present upon the rest of the stem, where petioles are red near the blade

only, where old tendrils are very red, where color is present in the hairs of leaves and not in the leaf surfaces, are unexplained by any theory ; also the appearance of red under the same conditions which usually favor the disappearance of color.

Stahl has given a plausible explanation of color in plants of the moist tropics, where color is located in the cells of tissues near the surface. Overton explains autumnal and spring coloration, but finds, although he can produce color in internal tissues of the plant, he is seldom able to do so in epidermal layers. None of the explanations given apply to all the cases here recorded.

In conclusion it is seen that the statistical observations presented fit no one theory in all particulars. Some facts agree with no theory at all so far as known. The suggestion may be made that with further experimental study red color may be found subserving a number of purposes or having a number of different meanings ; or, on the other hand, it may be due to an entirely unknown cause which may fit all cases.

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